

Additions to the Podostemaceae of Thailand with Molecular Phylogenetic Relationships of *Cladopus*, *Hydrobryum* and *Thawatchaia*

PETCHARAT WERUKAMKUL¹, LA-AW AMPORNPAN², MASAHIRO KATO³ AND SATOSHI KOI^{4,*}

¹Faculty of Science and Technology, Rajamangala University of Technology, Phra Nakhon, Bangkok 10800, Thailand; ²Department of Biology, Srinakharinwirot University, Bangkok 10110, Thailand; ³Department of Botany, National Museum of Nature and Science, Tsukuba 305-0005, Japan; ⁴Botanical Gardens, Faculty of Science, Osaka City University, Kisaichi, Katano, Osaka 576-0004, Japan.

*skoi@sci.osaka-cu.ac.jp (author for correspondence)

In this paper, based on recent collections, we add three species of Podostemaceae to the flora of Thailand. First, *Cladopus pierrei* was newly recorded from Sa Kaeo Province, southeastern Thailand. Phylogenetic analysis showed that *C. pierrei* is a paraphyletic species, in which plants from Thailand have a sister relationship with *C. doianus*. The number of stamens of *C. pierrei* in Thailand and Laos varies between 1 and 2, i.e., 2 in one clade, 1 in another clade, and 1 or 2 in a third clade. *Cladopus* is characterized by variation in stamen number. Second is *Hydrobryum chompuense* sp. nov. collected in Phitsanulok Province, northern Thailand. Phylogenetically, it is sister to *H. varium*, but morphologically distinct in having 1-locular ovaries with the septum free from the ovary wall. The third, *Thawatchaia laotica*, which has been reported from northern Laos, was newly recorded from Chiang Mai Province, northern Thailand. As a result, 10 genera and 52 species of Podostemaceae occur in Thailand.

Key words: *Cladopus pierrei*, *Hydrobryum chompuense*, Podostemaceae, Thailand, *Thawatchaia laotica*

Podostemaceae are aquatic and epilithic angiosperms comprising ca. 300 species assigned to ca. 54 genera in three subfamilies and distributed in the seasonal tropics and subtropics in Africa, Madagascar, America and Asia, but rare in Australia (Cook & Rutishauser 2007, Koi *et al.* 2012). The plants grow submerged in violent currents during the rainy season and produce flowers and fruits in the air in the dry season when water level is lower. Their morphology is specialized and adapted to the habitat where vertical growth of roots and shoots is restricted by rocks and currents (Rutishauser 1997, Cook & Rutishauser 2007, Kato 2013, 2016). The principal organ in most species is a procumbent, adhering root; a few species are rootless. The roots are subcylindrical, ribbon-like or crustose, and produce shoots and flowers adventitiously. The flowers are

generally simple, small and inconspicuous.

Recent taxonomic studies have revealed high diversity of Podostemaceae in Thailand, where there are 10 genera and 49 species (Kato 2004, 2006a, Kato & Koi 2009, Werukamkul *et al.* 2012, 2016). In Thailand, *Hydrobryum* contains the largest number of species, 15 (of 27 species worldwide) (Cusset 1992, Kato 2004, 2006a, 2008, Kato & Koi 2009, Koi & Kato 2012, 2015b, Werukamkul *et al.* 2012, 2016). *Thawatchaia* is closely related to *Hydrobryum* and forms a major clade with two other genera, *Hanseniella* and *Hydrodiscus* (Koi *et al.* 2012). *Thawatchaia* is bispecific consisting of *T. trilobata* M. Kato, Koi & Y. Kita, endemic to Thailand, and *T. laotica* Koi & M. Kato, endemic to Laos (Kato 2004, Werukamkul *et al.* 2012, 2016, Koi & Kato 2015b). *Cladopus* forms a major clade with *Paracladopus*.

This clade has a sister relationship with the clade consisting of *Hanseniella*, *Hydrobryum*, *Hydrodiscus*, and *Thawatchaia*. Nine species of *Cladopus* range from Thailand to Australia and Japan; two species have been reported for Thailand; *C. taiensis* C. Cusset, an endemic species (but recently collected in Cambodia, M. Kato unpubl. data), and *C. fallax* C. Cusset, which extends to southern Vietnam (Cusset 1973, 1992, Kato 2006b, 2011). Most species, i.e., *C. austrosinensis* M. Kato & Y. Kita, *C. fallax*, *C. nymanii* H. A. Möller, *C. queenslandicus* (Domin) C. D. K. Cook & Rutish., *C. taiensis*, have one stamen, *C. pierrei* has one or two stamens, and *C. doianus* (Koidz.) Koriba, *C. fukienensis* (H. C. Chao) H. C. Chao and *C. javanicus* M. Kato & Hambali have one stamen but occasionally two or more (Cusset 1973, 1992, Kato & Hambali 2001, Kato & Kita 2003, Kato 2006a, b, 2013, Koi & Kato 2010).

We here report one new species (*Hydrobryum chompuense*) and two new records, *Thawatchaia laotica* and *Cladopus pierrei*, for Thailand based on morphological and molecular phylogenetic data. As a result, 10 genera and 52 species are in Thailand.

Materials and Methods

Materials

Cladopus pierrei (Lecomte) C. Cusset, *Hydrobryum chompuense* (new species, see below), and *Thawatchaia laotica*, collected in Thailand and Laos, and new collections of other species in Thailand, were used for analysis (Appendix). The materials were stored in FAA (formalin : acetic acid : 50% ethanol = 5 : 5 : 90) for morphological analyses and in silica gel for DNA extraction. Vouchers were deposited in the Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand (BKF) and/or the Herbarium, Department of Botany, National Museum of Nature and Science, Tsukuba, Japan (TNS).

Morphology

We compared the morphology of newly collected specimens with the original description of *Cladopus pierrei*, *Thawatchaia laotica*, and closely related species (Imamura 1928, Koidzumi 1935, Chao 1948, Kato 2004, Kato *et al.* 2004, Koi & Kato 2012, Werukamkul *et al.* 2012, 2016, Koi & Kato 2015b). We observed 50 samples of each organ for *C. pierrei* (SK-04, SK-06, SK-07, SK-08) and *Hydrobryum chompuense* (TWA-337, TPK-205, TPK-206) and 20 samples for *T. laotica* (CM-13, TPK-103). Characters of *H. varium* Ampornpan, Werukamkul, Koi & M. Kato, which is most closely related to *H. chompuense*, were observed using 50 samples from specimens TWA-113 and TWA-114 (Table 2) and compared with the previous description (Werukamkul *et al.* 2012). The length of the filaments of *T. trilobata* was measured using specimens TWA-268, TWA-271, TWA-275, TWA-278, and TWA-281 because there are no descriptions from previous studies (Kato 2004, Kato *et al.* 2004, Werukamkul *et al.* 2012, 2016).

Phylogenetic analyses

In total, 118 samples were used for sequencing. The methods of DNA extraction, PCR amplification of chloroplast *matK* gene (1,518–1,587 bp), and sequencing were conducted following Koi & Kato (2010).

The sequences obtained in this study and those deposited in GenBank were used for phylogenetic analysis (Appendix). The sequences were aligned by CLUSTAL X (Thompson *et al.* 1997) and refined manually with MacClade 4.0 (Maddison & Maddison 2000). Gaps were treated as missing data. The program MrModeltest 2.3 (Nylander 2004) determined a general time reversible (GTR) + I (proportion of invariable sites) + G (shape parameter of the gamma distribution) substitution model as the best fitting model of substitution: nucleotide frequencies were A = 0.3283, C = 0.1463, G = 0.1247, T = 0.4007; the substitution rate matrix was A to C = 1.3516, A to G = 1.0633, A to T = 0.2971, C to G = 0.5316, C to T = 0.8416, G to T = 1.0000; the proportion of invariable sites was 0.2960; and the gamma distribution shape

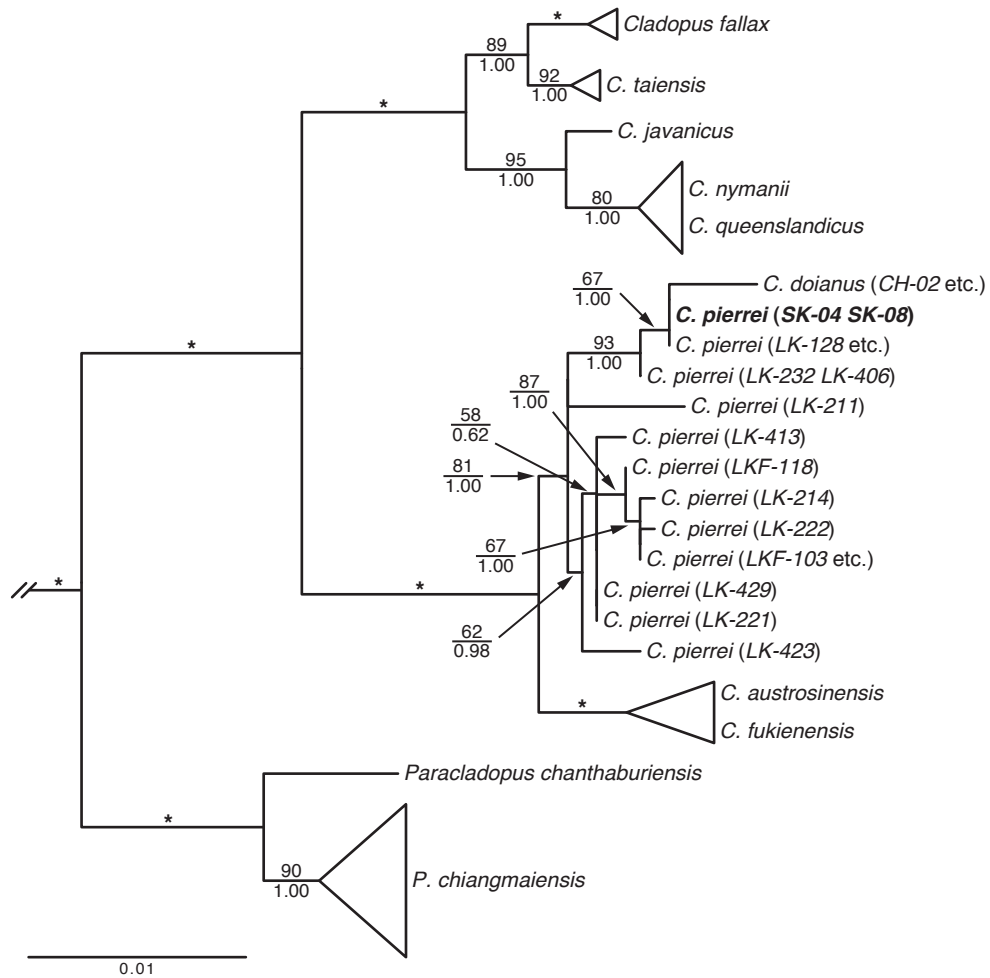


FIG. 1. ML phylogenetic tree of *Cladopus* deduced from *matK* sequences. Numbers above and below branches are ML bootstrap values (%) and Bayesian posterior probabilities, respectively. Asterisks indicate branches supported with 100% ML bootstrap value and 1.00 Bayesian posterior probability. For *C. pierrei*, accessions with prefixes LK and LKF are from Laos; accessions with prefix SK are from Thailand (Sakaeo). *Hanseniella*, *Hydrobryum*, *Hydrodiscus* and *Thawatchaia* are treated as outgroup (not shown; Koi *et al.* 2012). ‘CH-02 etc.’ consists of CH-02, JK-02, JP-127, JK-Anraku, JK-Manose, JK-Mawatari and JK-Yamazaki; ‘LK-128 etc.’ consists of LK-128, LK-132, LK-134, LK-237, LK-241, LK-419, and LK-433; and ‘LKF-103 etc.’ consists of LKF-103, LKF-109, LKF-120, LK-117, LK-121, LK-123 and LK-438.

parameter was 0.9530. Maximum likelihood (ML) analysis was conducted using RAxML-HPC2 (Stamatakis 2014) on XSEDE (8.2.6) in Cipres Science Gateway (Miller *et al.* 2010) with the GTR + I + G substitution model. Bootstrap probability values were calculated for 1,000 replicates. In the Bayesian analysis, the GTR + I + G model was used, and Markov chain Monte Carlo (MCMC) iterations with four chains were con-

ducted two times independently for 2,000,000 generations, sampling a tree every 100 generations, with the program MrBayes 3.2.5 (Ronquist *et al.* 2012). Potential scale reduction factors (PSRF) of all parameters approached 1.000 or 1.001 as runs converge. The first 5,000 trees were discarded as burn-in and the remaining 15,000 trees were used to determine the posterior probabilities for branches. *Cladopus* and *Paraclado-*

TABLE 1. Comparison of characters in *Cladopus pierrei* and *C. doianus*.

Character	<i>C. pierrei</i>		<i>C. doianus</i> **
	Thailand	Laos*	
Root	1–7 (median, 3) mm wide	1–4 (–7) mm wide	1–4 × 0.2–0.4 mm
Leaf	3–10 (8) per tuft, 1–11 (6) mm long	to 10 per tuft, to 3.5 mm long	3–15 per tuft, 3–8 mm long
Bract	8–12 (10), 0.7–2.7 (2) mm long	8–10, rarely 14, 1–2 mm long	8–15, 0.9–1.4 mm long, occasionally some of finger-like lobes to 11 mm long
Bract lobe	5–10 (8), 0.2–1.5 (1) mm long	5–10, 1–2 mm long	4–12, to 0.8 mm long
Spathella	1.5–2.8 (2.2) × 1–1.8 (1.3) mm	1.3–3.2 mm long	1.8–2 × 0.9–2 mm, apex mucronate
Pedice	2–5 (3) mm long	1–5 mm long	1–1.5 mm long
Tepal	0.5–1.2 (1) mm long	0.6–1.2 mm long	0.6–0.8 mm long
Stamen	1 (50%) or 2 (50%)***, 1.5–3 (1.8) mm long; if 2, forked 4/5 from base	1 or 2****, 1–3 mm long; if 2, forked above middle to near base	1, aberrantly forked, 0.8–1.3 mm long
Ovary	0.9–2 (1.1) × 0.6–1.5 (1) mm	0.9–2 × 0.6–1.6 mm	1.1–2.5 × 0.9–2.1 mm
Stigma	linear, subulate, 0.5–1 (0.6) mm long	linear or narrowly oblong, 0.5–1 mm long	narrowly fan-shaped with dilate apex, obovate-spatulate, or rhomboid-cuneate, 0.7–1.3 mm long
Ovule	14–48 (30) per locule	14–78 per locule	20–36 per locule
Capsule	1–2 (1.5) × 0.9–1.5 (1.2) mm	0.9–2 × 0.7–1.5 mm	1–2 × 1–2 mm
Stalk of capsule	3–8.5 (5) mm long	1–5 mm long	1.4–5 mm long

*Data are based on Koi & Kato (2012) and present study.
**Data are based on Imamura (1928), Doi (1929), Koidzumi (1935), Chao (1948) and present study.
***Number of flowers examined: *N* = 50; 10 flowers with one stamen and 10 flowers with two stamens among 20 samples of specimen SK-04, and 15 flowers with one stamen and 15 flowers with two stamens among 30 samples of SK-08.
****Flowers with one stamen in 14 accessions and two stamens in 8 accessions (see in the text; Koi & Kato 2012, Koi & Kato unpubl. data).

pus species were treated as outgroup for the phylogenetic tree of *Hanseniella*, *Hydrobryum*, *Hydrodiscus* and *Thawatchaia*, and vice versa.

Estimation of conservation status

IUCN categories (IUCN 2014) were assigned to each species for a preliminary conservation status.

Results and Discussion

ML analysis and two independent Bayesian analyses showed the same phylogenetic topology among the species examined, except *LK-221* of *Cladopus pierrei*. The specimen *LK-221* was placed outside the clade comprising *LK-214*, *LK-222*, *LK-413*, *LKF-118* and ‘*LKF-103* etc.’ (= *LKF-*

103, *LKF-109*, *LKF-120*, *LK-117*, *LK-121*, *LK-123* and *LK-438*) in ML tree (Fig. 1), while it was included within the clade supported with unreliable posterior probability (0.56) in the Bayesian trees (data not shown). The specimens of *Cladopus pierrei* collected in Thailand, i.e., *SK-04*, *SK-08*, were identical in *matK* sequences. ML analysis showed that the two specimens were nested in the clade comprising *C. pierrei* and *C. doianus* supported with 93% ML bootstrap value and 1.00 Bayesian posterior probability (Fig. 1). Within the clade, the Thai specimens formed a monophyletic clade with Lao specimens *LK-128*, *LK-132*, *LK-134*, *LK-232*, *LK-237*, *LK-241*, *LK-406*, *LK-419*, and *LK-433*, and *C. doianus* from China (*CH-02*) and Japan (*JK-02*, *JP-127*, *JK-Anraku*, *JK-Manose*, *JK-Mawatari* and *JK-Yamazaki*). This clade was distinct from the other Lao speci-

mens of *Cladopus pierrei*.

Among the *Cladopus pierrei* specimens, *SK-04* and *SK-08* of Thailand (Sa Kao), ‘*LK-128* etc.’, and *LK-232* and *LK-406* of Laos (Salavan and Attapeu) formed a monophyletic clade together with *C. doianus* of eastern-central China (Fujian) and southwestern Japan (Kyushu) supported with 93% ML bootstrap value and 1.00 Bayesian posterior probability (Fig. 1). Another clade consisted of only *LK-211*, the rest consists of *LK-423*, *LK-429*, *LK-221*, *LK-413*, *LKF-118*, *LK-222*, ‘*LKF-103* etc.’ and *LK-214*. Thus, *C. pierrei* was paraphyletic to *C. doianus*, reinforcing the preliminary data of Koi *et al.* (2012). While similar in most characters, *C. pierrei* differed from *C. doianus* in the stamen and stigma: the stamen was one or two in *C. pierrei* versus one or occasionally two or more (in *C. doianus*); and the stigma was subulate, linear, or narrowly oblong versus narrowly fan-shaped, obovate-spatulate, or rhomboid-cuneate (Table 1).

In *Cladopus pierrei* of Thailand (*SK-04*, *SK-08*), flowers with two stamens were as frequent as flowers with 1 stamen. The number of stamens is also various in *C. doianus* of Japan and *C. pierrei* of Laos: *C. doianus* has one or occasionally two or more (Doi 1929); and *C. pierrei* has two (*LK-128*, *LK-132*, *LK-134*, *LK-211*, *LK-232*, *LK-237*, *LK-241*, *LK-419*) or one (*LK-117*, *LK-121*, *LK-123*, *LK-214*, *LK-221*, *LK-222*, *LKF-103*, *LKF-109*, *LKF-118*, *LKF-120*, *LK-413*, *LK-423*, *LK-426*, *LK-429*) (Koi & Kato 2012; S. Koi & M. Kato unpubl. data). In the present tree (Fig. 1), *C. pierrei* of Thailand belonged to the clade of *C. doianus* and *C. pierrei* with two stamens. This variation and phylogeny support Koi & Kato (2012), who rejected Cusset’s (1992) characterization of *Cladopus* sect. *Griffithella* as having two stamens, excluded the section from *Cladopus*, and redefined *Cladopus* as having one or two stamens.

Hydrobryum chompuense, *TWA-337*, was phylogenetically sister to *H. varium* (*TPK-22*), but the two were distinct in *matK* sequences, i.e., 27 bp of 1,542 bp including 12 gaps were different (Fig. 2).

Specimens *CM-13* and *TPK-103* merged in *Thawatchaia laotica* with little sequence varia-

tion. The clade of *T. laotica* was robustly supported (100% bootstrap value and 1.00 Bayesian posterior probability) and separated from the clade of *T. trilobata* (Fig. 3).

Morphologically, *Cladopus pierrei* (photographs of Thai specimen are shown in Fig. 4) and *Thawatchaia laotica* from Thailand are conspecific.

Revised keys to all species of Podostemaceae in Thailand, including the new records and new species, will appear in the Flora of Thailand treatment (M. Kato, in preparation).

Taxonomic treatment

Cladopus pierrei (Lecomte) C. Cusset, Fl. Cambodge, Laos & Vietnam 14: 73, pl. 10, f. 7–9 (1973); *Mniopsis pierrei* Lecomte, Notul. Syst. (Paris) 1(1): 8–10. 1909.—*Griffithella pierrei* (Lecomte) Engl., Nat. Pflanzenfam., ed. 2 [Engler & Prantl] 18a: 61 (1930). *Typus*. Laos, Champasac, Bassac, *F.(A.) F. J. Harmand 5194* (holotype).—Fig. 4, Table 1

Distribution. Central and southern Laos, southern Vietnam and southeastern Thailand (Fig. 5). In Thailand, it has been collected at four places in one river in Pang Sida National Park, Sa Kao Province (Fig. 5). The plants are sympatric with *Hydrobryum khaoyaiense* M. Kato in Mantara waterfall (*SK-04*) and Kaeng Dan Krating (*SK-08*), where *C. pierrei* was more dominant than *H. khaoyaiense*. In the other two locations (*SK-06*, *SK-07*), only *C. pierrei* was sparsely distributed.

Preliminary conservation status. The species is known from four collections in the same river along 14°07' N latitude in Thailand and one collection in southern Vietnam (Cusset 1992, Kato 2011), but rather widely distributed in Laos (Koi & Kato 2012). Therefore, the conservation status is suggested as Least Concern.

Specimens examined. Southeastern Thailand, Sa Kao Prov., Pang Sida National Park: Mantara waterfall, 14°07'34.5" N, 102°13'23.7" E, 280 m alt., 28 Jan. 2012, st.

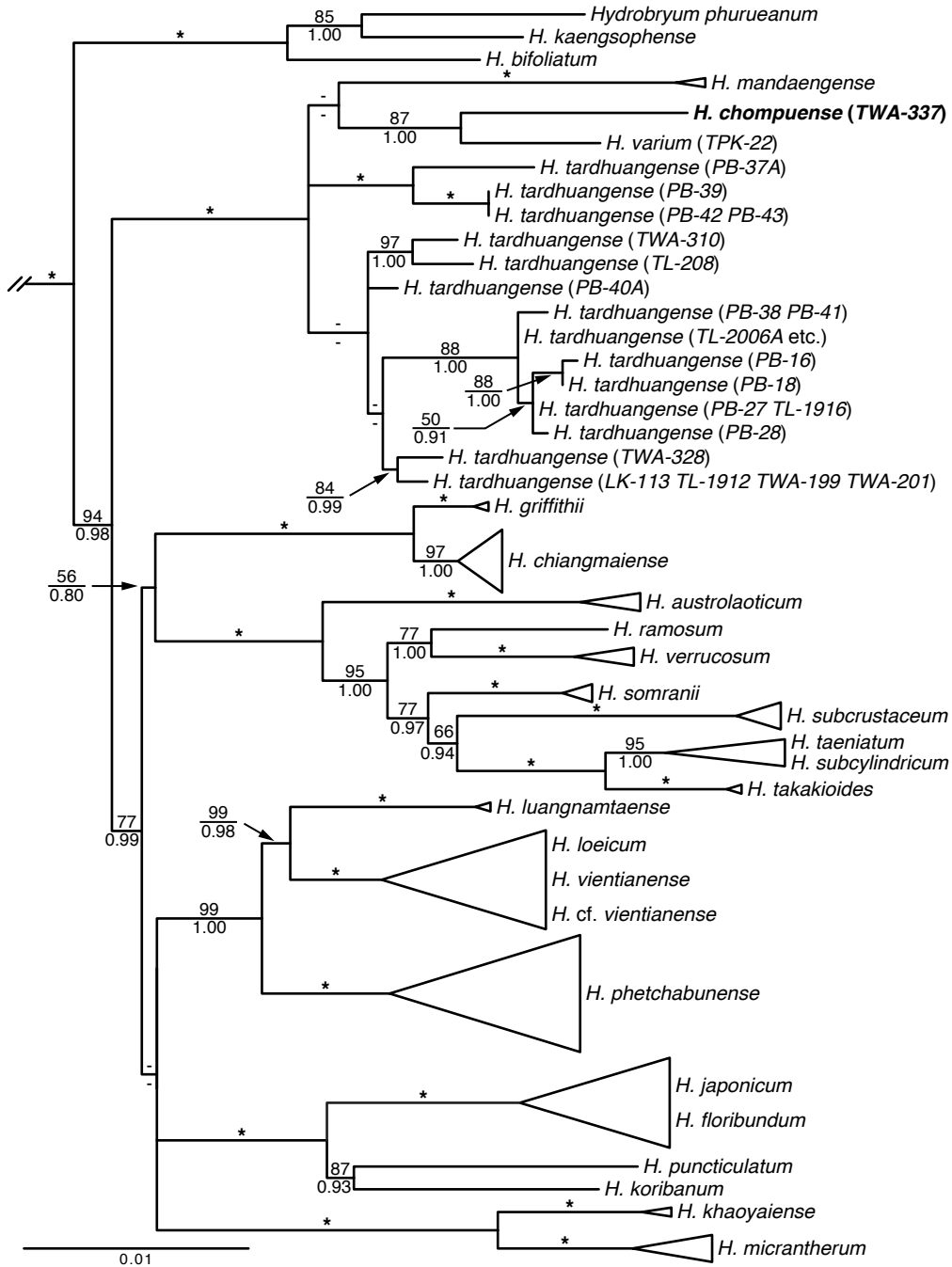


FIG. 2. ML phylogenetic tree of *Hydrobryum* deduced from *matK* sequences. Numbers above and below branches are ML bootstrap values (%) and Bayesian posterior probabilities, respectively. Asterisks indicate branches supported with 100% ML bootstrap value and 1.00 Bayesian posterior probability. Materials are given in brackets following species names. *Cladopus* and *Paracladopus* are treated as outgroup (not shown; Koi *et al.* 2012). 'TL-2006A etc.' consists of PB-26, PB-29, PB-44, TL-2006A, TL-2007 and TL-2009.

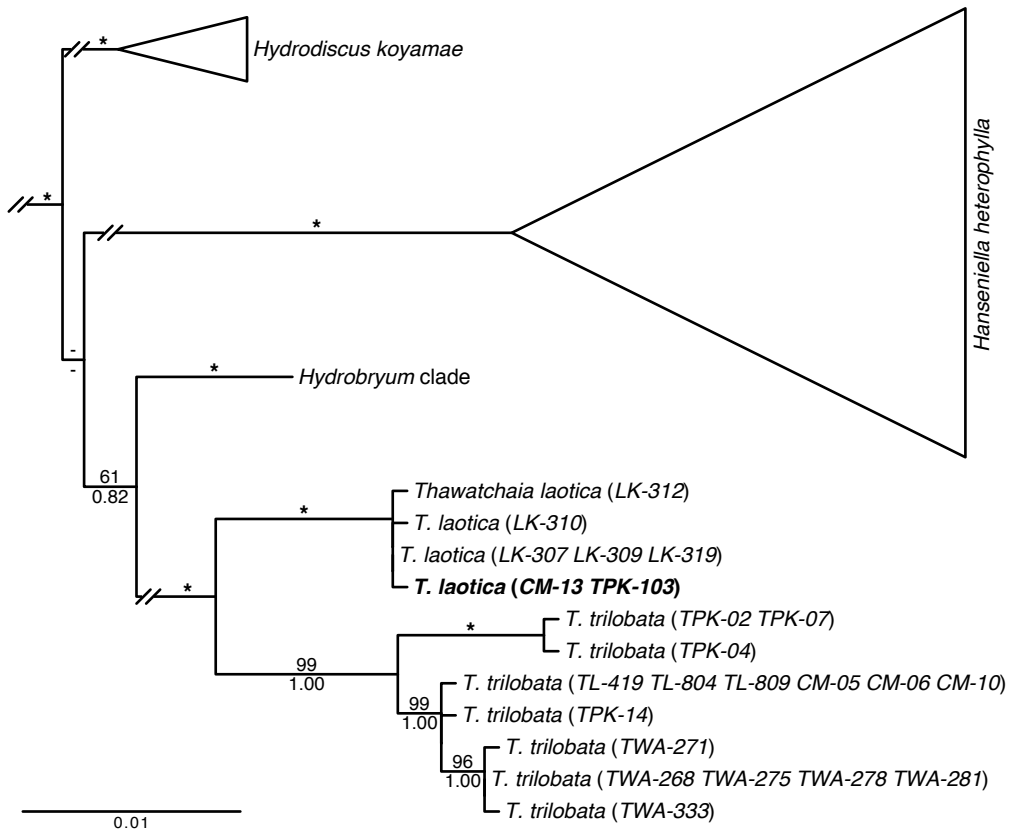


FIG. 3. ML phylogenetic tree of *Hanseniella*, *Hydrobryum*, *Hydrodiscus* and *Thawatchaia* deduced from *matK* sequences. Numbers above and below branches are ML bootstrap values (%) and Bayesian posterior probabilities, respectively. Asterisks indicate branches supported with 100% ML bootstrap value and 1.00 Bayesian posterior probability. Materials are given in brackets following species names. *Thawatchaia laotica*, CM-13 was collected in Thailand, the others are from Laos. All materials of *T. trilobata* was collected in Thailand. *Cladopus* and *Paracladopus* are treated as outgroup (not shown; Koi *et al.* 2012).

fl. fr., *P. Werukamkul* & *L. Ampornpan* SK-04 (BKF, TNS); loc. *ibid.*, Suanman Suantong waterfall, 14°07'26.7" N, 102°13'15.1" E, 204 m alt., 29 Jan. 2012, fr., *P. Werukamkul* & *L. Ampornpan* SK-06 (BKF, TNS); loc. *ibid.*, Khwae Makha waterfall, 14°07'14.2" N, 102°12'32.3" E, 187 m alt., 29 Jan. 2012, fl. fr., *P. Werukamkul* & *L. Ampornpan* SK-07 (BKF, TNS); loc. *ibid.*, Kaeng Dan Krating, 14°07'31.8" N, 102°12'50.1" E, 368 m alt., 30 Jan. 2012, st. fl. fr., *P. Werukamkul* & *L. Ampornpan* SK-08 (BKF, TNS).

Notes. In addition to *Cladopus taiensis* and *C. fallax*, *C. pierrei* is the third species of *Cladopus* in Thailand (Cusset 1973, 1992, Kato 2006a, present study). Among these species, *C. taiensis* is recognized by bracts divided into 2–5 obtuse, deltoid, smooth-surfaced lobes and having one

stamen. *Cladopus fallax* and *C. pierrei* have digitate bracts with a rough surface. *Cladopus pierrei* is distinguished from *C. fallax* by having one or two stamens, more bracts, bracts divided into more finger-like lobes, more ovules per locule, and much longer pedicels and capsule stalks (Fig. 4).

Hydrobryum chompuense Werukamkul, Ampornpan, M. Kato & Koi, **sp. nov.**—Fig. 6

Differs from the closely related *Hydrobryum varium* in the ovate or broadly ovate bracts with acute, acuminate or caudate apex, tail like tip caducous when apex caudate, shorter pedicels, shorter stamens, shorter andropodia, 1-locular ovary with incomplete septum separated from

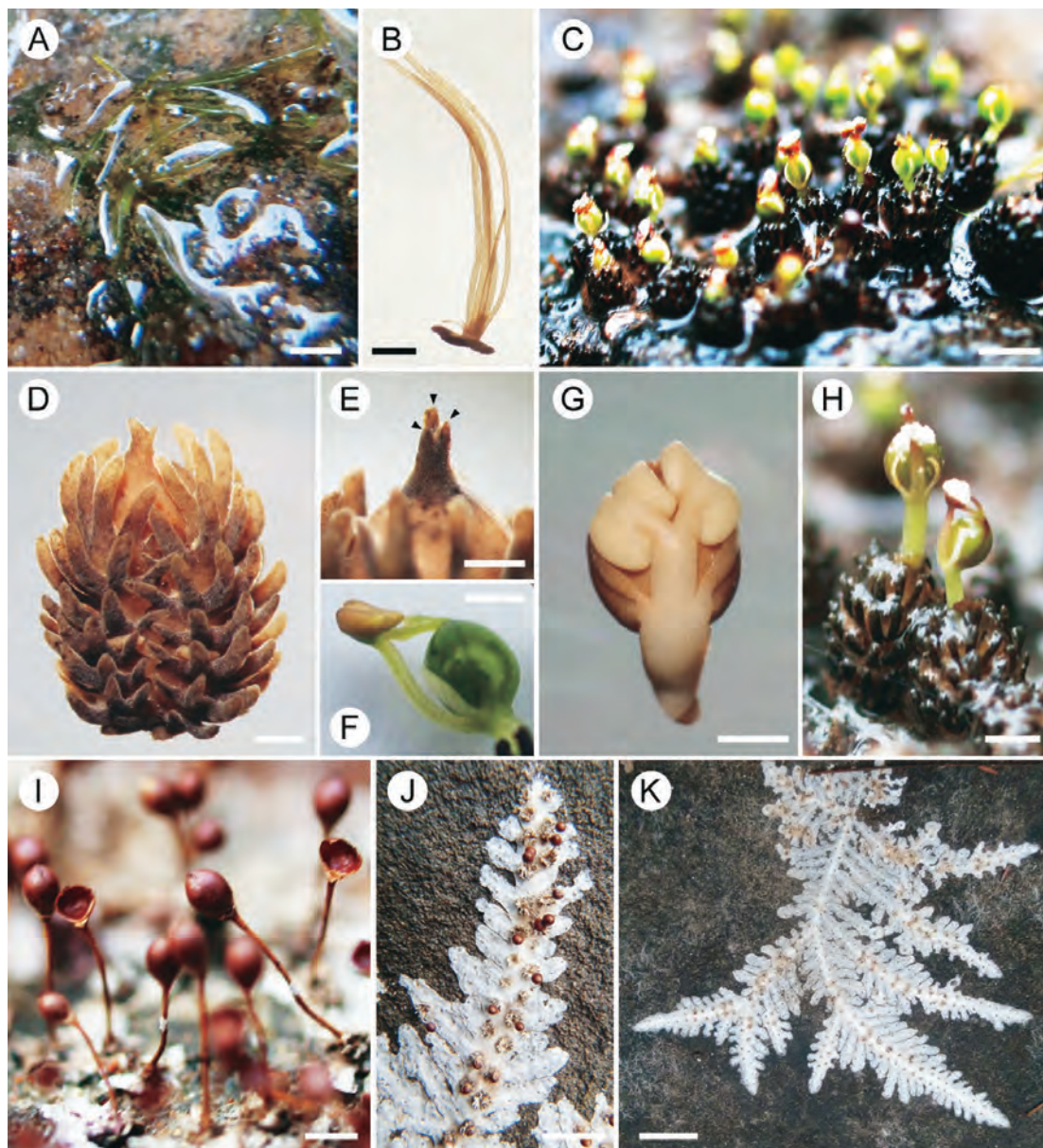


FIG. 4. Photographs of *Cladopus pierrei* in nature (A, C, H–K) and under light microscope (B, D–G). A. Tufts of leaves under water. B. Tuft of leaves on dorsal surface of root. C. Flowers at anthesis. D. Reproductive shoot with digitate bracts and terminal floral bud enclosed by spathe with two-tipped mucro. E. Terminal floral bud enclosed by spathe with three-tipped mucro (arrowheads). F. Flower prior to anthesis (spathe removed) seen from side showing single stamen and two stigmas. G. Flower with two stamens (spathe removed). H. Two flowers with single stamen releasing pollen from anthers; two tepals on sides of stamen. I. Stalked capsules. Two dehiscent capsules with persistent capsule valves. J. Dried root with scars of reproductive shoots on dorsal surface near sinuses of root branches. K. Dried branched ribbon-like root creeping on rock surface. Brown spots along parent roots are scars of reproductive shoots. Scale bars = 2 mm in A, C, H, I; 1 mm in B, F; 500 μ m in D, E, G; 2 cm in J; 1 cm in K.

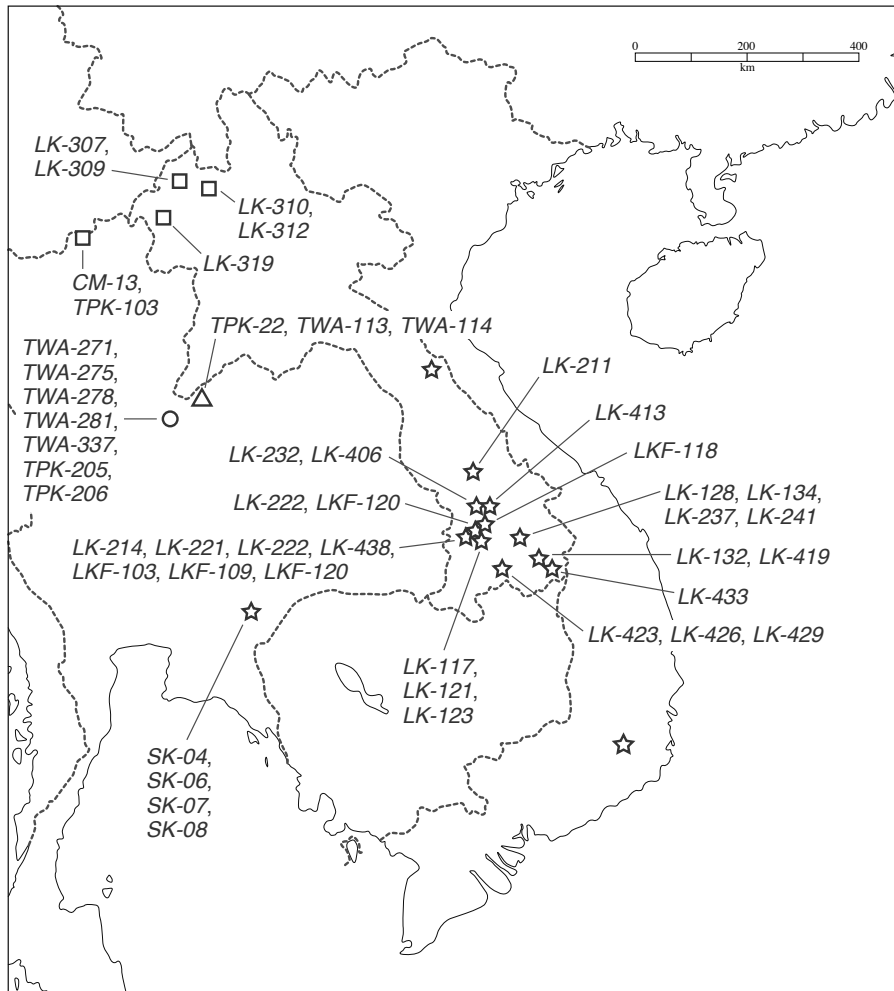


FIG. 5. Map of Southeast Asia showing locations of *Cladopus pierrei* (marked by stars), *Hydrobryum chompuense* (circle), *H. varium* (triangle), and *Thawatchaia laotica* (squares).

ovary wall, and smaller ovaries and capsules (Table 2).

Typus. Northern Thailand. Phitsanulok Province, Noen Maprang Dist., Tung Salaeng Luang National Park, Khlong Chompu stream, Kaeng Tham Namnoi, 16°40'01.0" N, 100°46'02.3" E, 131 m alt., 9 Dec. 2016, st. fl. fr., P. Werukamkul, L. Ampornpan & S. Koi TPK-205 (holo- BKF; iso- TNS).

Roots crustose, 0.1–0.5 (median, 0.2) mm thick, tightly attached to rock surface by adhesive hairs on the lower surface, irregularly lobed, lobes 3–8 (5) mm wide. Leaves needle-like, 0.6–3.5 (1.5) mm long, apex acute, tufted on dorsal surface, 2–5 (3) per tuft. Flowering shoots (consisting of bracts and spathe, in which mature

flower is enveloped) appressed to the root surface, 1–1.6 (1.2) mm long; bracts 2–4 (2) in 2 ranks, imbricate, 0.4–4.3 (1) mm long (0.3–1 (0.6) mm long without tail like tip of 0.2–4 (2) mm long), 0.2–0.8 (0.5) mm wide, ovate, broadly ovate or semicircular, sheath-like, papillate in lower part, apex acute, acuminate or caudate, tail like tip caducous when apex caudate; spathe enclosing flower bud, ellipsoidal, flattened, papillate conspicuously in marginal part, 0.9–1.7 (1.5) mm long, 0.9–1.5 (1.1) mm wide, ruptured longitudinally at anthesis. Flowers single, terminal, oblique to erect; pedicel 0.2–0.5 (0.4) mm long; tepals 2, each on either side of stamen, linear,

TABLE 2. Comparison of *Hydrobryum chompuense* and *H. varium*.

Character	<i>H. chompuense</i>	<i>H. varium</i> *
Root	0.1–0.5 (median 0.2) mm thick	0.1–0.2 (median, 0.1) mm thick
Leaf	2–5 (3) per tuft, 0.6–3.5 (1.5) mm long,	1–3 (2) per tuft, 1.5–3.5 (1.5) mm long, surrounded by raised ring of root tissue
Flower shoot**	1–1.6 (1.2) × 0.9–1.2 (1) mm	1.4–2 (1.8) × 0.7–1.2 (1) mm
Bract	2–4 (2), 0.4–4.3 (1) × 0.2–0.8 (0.5) mm, ovate, broadly ovate or semicircular, sheath-like, apex acute, acuminate or caudate, tail like tip caducous when apex caudate	2–4 (2), 0.5–0.8 (0.5) × 0.3–0.5 (0.5) mm, deltoid, sheath-like, apex acuminate
Pedicel	0.2–0.5 (0.4) mm long	0.6–2 (1.1) mm long
Tepal	1.2–2.5 (1.6) mm long	1.6–2.6 (2) mm long
Stamen	2; 2.8–5.0 (3.5) mm long	2; 3.5–6 (4.5) mm long
Common stalk of filaments (= andropodium)	1.2–2.5 (1.8) mm long	2.5–4.5 (4) mm long
Ovary	1–1.6 (1.5) × 0.6–1 (0.7) mm; 1-locular	1.5–2.5 (2) × 0.8–1.2 (0.9) mm; 2-locular
Septum	separated from ovary wall	connected to ovary wall
Gynophore	0.3–1 (0.6) mm long	0.5–1.6 (1) mm long
Stigma	0.3–1 (0.5) mm long, linear or lanceolate, apex acute	0.5–1.4 (0.8) mm long***, linear, apex acute
Ovule	16–40 (26) per ovary, on margin of placenta and occasionally with 1–5 ovules in upper central area	(11–)23–37 (22) per locule, on most surface of septum
Capsule	1–2 (1.5) × 0.7–1 (0.8) mm	1.5–2.8 (2) × 0.8–1.2 (1) mm
Stalk of capsule	0.6–1.2 (1) mm long	1.5–3.6 (2.6) mm long
No. of capsule ribs	12–16 (12)	12–14 (12)
Seed	0.24–0.38 (0.32) × 0.09–0.24 (0.16) mm	0.25–0.35 (0.3) × 0.12–0.2 (0.18) mm

*Data are basically from Werukamkul *et al.* (2012). Data in italic are revisions based on recent collections (see Materials & Methods).

**Flower shoots consist of bracts and mature flower enveloped within spathella.

***Longer stigma 0.6–1.4 mm long, shorter one 0.5–1.2 mm (Werukamkul *et al.* 2012).

1.2–2.5 (1.6) mm long, apex acute, lower than ovary; stamens 2, 2.8–5.0 (3.5) mm long, longer than pistil, forked 1/2 from tip, filaments 2.5–4.7 (3.3) mm long, distal part of filament 1–2.5 (1.6) mm long, proximal part (= andropodium) 1.2–2.5 (1.8) mm long; anthers oblong or broadly oblong, 0.3–0.4 (0.4) mm long, 0.3–0.4 (0.3) mm wide, basifixed, thecae equal or subequal in length, tetrasporangiate, apex truncate, base obtuse, dehiscing introrsely and longitudinally, pollen in dyads; gynophore 0.3–1 (0.6) mm long; ovary 1, ellipsoid, flattened, 1–1.6 (1.5) mm long, 0.6–1 (0.7) mm wide, 1-locular with incomplete septum separate from ovary wall; ovules 16–40 (26) per ovary, borne on the margin of placenta surface, occasionally with 1–5 ovules in upper central area; stigma 0.3–1 (0.5) mm long, bifid below middle, lobes linear or lanceolate, subequal or unequal, apex acute, papillate, ventral lobe thick-

er than dorsal one; capsules stalked (stalk 0.6–1.2 (1) mm long), ellipsoid, flattened, 1–2 (1.5) mm long, 0.7–1 (0.8) mm wide, ribs 12–16 (12), dehiscing by two equal valves, valves persistent; seeds 5–30 (16) per capsule, flattened, elliptical ovate, 0.24–0.38 (0.32) mm long, 0.09–0.24 (0.16) mm in diam.

Distribution. Known only from Phitsanulok Province, northern Thailand (Fig. 5). *Hydrobryum chompuense* is sympatric with *Dalzellia sparsa* Ampornpan, Werukamkul, M. Kato & Koi, *Terniopsis minor* M. Kato & Koi and *Hydrobryum phetchabunense* M. Kato & Koi. The extent of occurrence and area of occupancy are estimated to be 4,173 m² and 450 m², respectively.

Preliminary conservation status. Vulnerable (VU D2)

Other specimens examined. Northern Thailand, Phit-

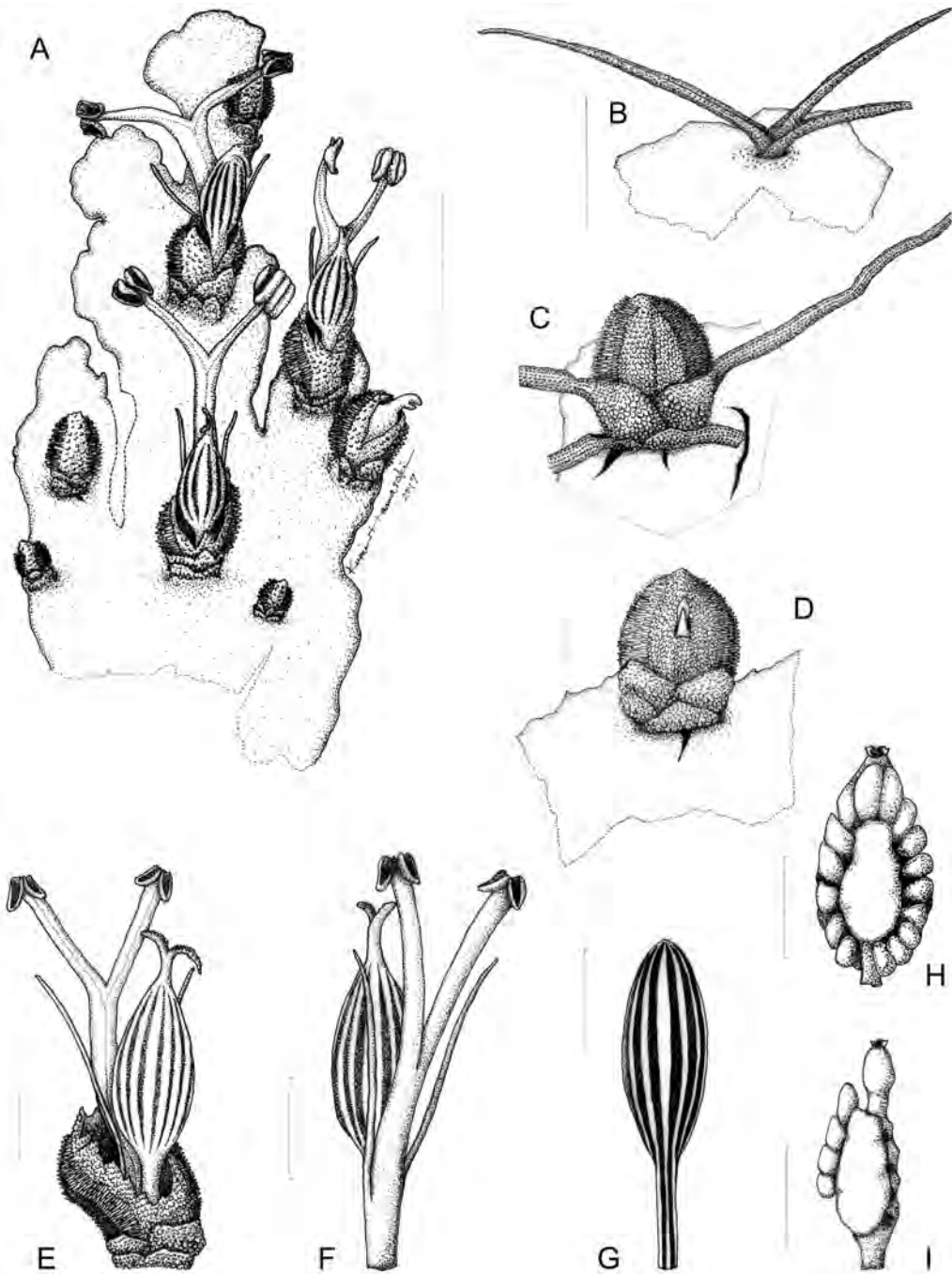


FIG. 6. *Hydrobryum chompuense* (TWA-337 and TPK-205). A. Crustose lobed root with flowers and flower buds on dorsal surface. B. Tuft of leaves. C. Flower bud subtended by bracts with caudate apex. Young flower enclosed by spathe with papillate margin. D. Flower bud subtended by bracts with acute apex. Note that spathe is ruptured longitudinally and stigma is visible. E. Flower extruded from ruptured spathe subtended by bracts: dorsal view. F. Flower: ventral view. G. fruit. H. Ovules on margin (not seen) of septum. I. Incomplete septum with reduced margin; most ovules removed. Scale bars = 3 mm in A; 1 mm in B–I.

TABLE 3. Comparison of species of *Thawatchaia*.

Character	<i>T. laotica</i>		<i>T. trilobata</i> ^{*2}
	Thailand	Laos ^{*1}	
Root	crustose, irregularly lobed, 0.2–0.4 mm thick	crustose, irregularly lobed, 0.3–0.4 mm thick	crustose, irregularly lobed, 0.2–0.6 mm thick
Bract	4–8, trilobed; dorsal and middle lobes narrowly deltoid, acute; ventral lobe semicircular, much shorter than dorsal and middle lobes	(4–)6–10, trilobed; dorsal and middle lobes narrowly deltoid, bluntly acute; ventral lobe semicircular, much shorter than dorsal and middle lobes	4–6 per rank, trilobed; lobes bluntly acute ^{*3} ; ventral lobe obtuse, shorter than dorsal and middle lobes
Pedicel	0.4–0.9 mm long	0.2 mm long	0.6–1 mm long ^{*4}
Gynophore	0.7–1.1 mm long	0.5–0.8 mm long	1–1.7 mm long ^{*4}
Tepal	2.5–3 mm long	2–3.5 mm long	2–4 mm long ^{*5}
Stamen	2; 3–3.8 mm long	2; 2.5–3 mm long	2; 3–7 mm long ^{*6} , as long as, or longer than ovary ^{*7}
Filament	2.8–3.3 mm long, forked near or above middle	forked 4/5–5/6 from base	2.7–6.2 mm long, forked near or above middle ^{*8}
Anther	0.5–1 mm long, 0.3–0.6 mm wide	0.5–0.8 mm long	ca. 1.2 mm long ^{*9}
Ovary	ellipsoid, slightly flattened, 1.5–2.2 mm long, 0.8–1 mm in diam.; 2-locular	ellipsoid, 2–2.2 mm long, 0.8–1 mm in diam.; 2-locular	ellipsoid, flattened, 2–3.5 mm long ^{*10} , 1–1.5 mm in diam. ^{*11} ; 2-locular
Stigma	2; linear, 0.8–1.2 mm long	2; linear, to 1.2–1.5 mm long	2; linear, 0.5–2 mm long ^{*12}
Ovule	7–16 per locule, on whole surface of septum except in lower central area	8–16 per locule, on whole surface of septum except in lower central area	4–9(–11) per locule ^{*13} , on marginal surface of septum or whole surface except in small lower central area ^{*14}
Stalk of capsule	1.5–2 mm long	1.5–2 mm long	2–3 mm long
Capsule	ellipsoid, slightly flattened, 2–2.2 mm long, 0.9–1.1 mm in diam.	ellipsoid, slightly flattened, 2–2.2 mm long, 0.9–1 mm in diam.	ellipsoid, flattened ^{*15} , 2–3.5 mm long, 1–1.5 mm in diam. ^{*16}
No. of capsule ribs	8	7–8	8–10

^{*1} Data are based on Koi & Kato (2015b).

^{*2} Data are from Kato *et al.* (2004), Kato (2004) and Werukamkul *et al.* (2012, 2016). Added data are shown in italics.

^{*3} Dorsal and middle lobes acute; ventral lobe obtuse (Werukamkul *et al.* 2012).

^{*4} Length of ovary stalk (= pedicel + gynophore) 2–3.5 mm long (Kato *et al.* 2004).

^{*5} 2–3.5 mm long (Kato *et al.* 2004); 2.5–4 mm long (Werukamkul *et al.* 2012).

^{*6} 3–5(–7) mm long (Kato *et al.* 2004); 6–7 mm long (Werukamkul *et al.* 2012).

^{*7} Longer than ovary (Kato *et al.* 2004).

^{*8} Forked above middle (Werukamkul *et al.* 2012).

^{*9} No description in Werukamkul *et al.* 2012.

^{*10} 2.5–3.5 mm long (Kato *et al.* 2004); 2–3 mm long (Werukamkul *et al.* 2012).

^{*11} No description of width of ovary in Kato *et al.* 2004.

^{*12} 0.6–1 mm long (Kato *et al.* 2004); 0.5–2 mm long (Werukamkul *et al.* 2012).

^{*13} 7–9(–11) per locule (Kato *et al.* 2004); 6–8 per locule (Werukamkul *et al.* 2012); 4–8 per locule (Werukamkul *et al.* 2016).

^{*14} Ovules borne on marginal surface of septum except in sterile middle area (Werukamkul *et al.* 2012).

^{*15} Kato *et al.* 2004.

^{*16} 2–3 mm long and 1 mm wide (Kato *et al.* 2004); 2.5–3.5 mm long and 1–1.5 mm wide (Werukamkul *et al.* 2012).

sanulok Prov., Noen Maprang Dist., Tung Salaeng Luang National Park, Khlong Chompu stream: Kaeng Tham Namnoi, 16°40'01.0" N, 100°46'02.3" E, 131 m alt., 3 Mar. 2015, fl. fr., *P. Werukamkul* & *L. Ampornpan* TWA-337 (BKF, TNS); loc. *ibid.*, Kaeng Tham Namnoi, 9 Dec. 2016, st. fl. fr., *P. Werukamkul*, *L. Ampornpan* & *S. Koi* TPK-205 (BKF, TNS); loc. *ibid.*, Kaeng Hinlad, 16°39'43.6" N, 100°46'01.0" E, 153 m alt., 9 Dec. 2016, st. fl. fr., *P. Werukamkul*, *L. Ampornpan* & *S. Koi* TPK-206 (BKF, TNS).

Notes. *Hydrobryum chompuense* has the smallest vegetative and reproductive organs among the congeners in Thailand. It is similar to *H. somranii* in Thailand and *H. subcrustaceum* in Laos in the crustose roots and flowers with 2 stamens and 1-locular ovary, although the former is not closely related to the latter two species (Fig. 2; Kato 2004, Koi & Kato 2012). *Hydrobryum chompuense* differs from *H. somranii* and *H. sub-*

crustaceum in the acute, acuminate or caudate apex of the bracts (vs. obtuse) and the unequal or subequal stigma lobes (vs. equal). Furthermore, *H. subcrustaceum* has distinguishable floral characteristics: sessile flowers, ovary embedded within spathe at anthesis (i.e., only stamens and stigmas emerging), and capsules ripened within persisted spathe (Koi & Kato 2012).

Hydrobryum chompuense is sympatric with *H. phetchabunense* at the type locality. It is distinguished by the acute, acuminate or caudate (tail like tip caduceus when caudate) apex of the bracts in the former vs. obtuse in the latter, spathe ruptured longitudinally at anthesis vs. irregularly, pedicels 0.2–0.5 mm long vs. 0.5–2.5 mm long, ovary 1-locular vs. 2-locular, and the stalk of capsules 0.6–1.2 mm long vs. 1–6 mm long (Werukamkul *et al.* 2016).

Thawatchaia laotica Koi & M. Kato in Acta Phytotax. Geobot. 66: 181, f. 1 (2015).

Distribution. Northern Thailand (Chiang Mai) and northern Laos (Luang Namtha, Bokeo); these localities are rather close to each other. We found sparse colonies in Thailand on three rocks in a small population in 2014. During our visit in 2016 we found the plants on one rock had vanished, indicating that the population fluctuates on a small scale. The extent of occurrence in Thailand is estimated to be 200 m².

Preliminary conservation status. Near Threatened (NT).

Specimens examined. Northern Thailand, Chiang Mai Prov., Mae Ai Dist., Kok river, Kaeng Yung, 20°04'17.2 N, 99°21'31.6 E, 457 m alt., 4 Apr. 2014, fl. fr., P. Werukamkul & L. Ampornpan CM-13 (TNS); loc. *ibid.*, 18 Jan. 2016, fl. buds, fl. fr., P. Werukamkul, L. Ampornpan & S. Koi TPK-103 (TNS).

Notes. *Thawatchaia* is bispecific. *Thawatchaia trilobata* occurs in northern (Chiang Mai, Phitsanulok) and northeastern (Loei) Thailand (Kato *et al.* 2004, Kato 2004, Werukamkul *et al.* 2012, 2016), and *T. laotica* occurs in north-

ern Laos (Luang Namtha, Bokeo) (Koi & Kato 2015b) and northern Thailand (Chiang Mai) (present study). *Thawatchaia laotica* differs from *T. trilobata* in the remarkably asymmetric lobed bracts with a semicircular ventral lobe (vs. acute in *T. trilobata*) (Table 3; Koi & Kato 2015b). They are also distinct in the *matK* sequences (Fig. 3; Koi *et al.* 2012).

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APPENDIX. Materials used in this study. Species names are followed by author(s), locality, vouchers with herbarium acronyms, and GenBank accession numbers of *matK*. Full data are shown for materials that were collected in this study, while localities (province and country), collection numbers of vouchers, and GenBank accession numbers are shown for the other materials [for sources of their GenBank accession numbers, see Koi *et al.* (2012)]. Some specimens were used only for morphological observations.

- Cladopus austrosinensis* M. Kato & Y. Kita—Hainan, China, *CH-301* (AB104560); Guangdong, China, *CH-302* (AB104559). *Cladopus doianus* (Koidz.) Koriba—Fujian, China, *CH-02* (AB179654); Kagoshima, Japan, *JK-02* (AB038189); Kagoshima, Japan, *JK-Anraku* (AB038189); Kagoshima, Japan, *JK-Manose* (AB179656); Kagoshima, Japan, *JK-Mawatari* (AB179655); Kagoshima, Japan, *JK-Yamazaki* (AB038189); Miyazaki, Japan, *JP-127* (AB698209). *Cladopus fallax* C. Cusset—Trat, Thailand, *TKF-109* (AB698210); Chanthaburi, Thailand, *TL-701* (AB293561); Trat, Thailand, *TL-1610* (AB537378). *Cladopus fukienensis* (H. C. Chao) H. C. Chao—Fujian, China, *CH-01* (AB179653); Kagoshima, Japan, *JK-03* (AB048371). *Cladopus javanicus* M. Kato & Hambali—West Java, Indonesia, *ID-02* (AB066175). *Cladopus nymani* H. Möller—Flores Island, Indonesia, *FL-02* (AB698211); West Java, Indonesia, *ID-03* (AB104561); Sulawesi, Indonesia, *S-01* (AB104577). *Cladopus pierrei* C. Cusset—Champasak, Laos, *LK-117* (AB610213); Champasak, Laos, *LK-121* (AB610214); Champasak, Laos, *LK-123* (AB610215); Attapeu, Laos, *LK-128* (AB610219); Attapeu, Laos, *LK-132* (AB610220); Attapeu, Laos, *LK-134* (AB610221); Savannakhet, Laos, *LK-211* (AB610224); Champasak, Laos, *LK-214* (AB610225); Champasak, Laos, *LK-221* (AB610226); Champasak, Laos, *LK-222* (AB610227); Salavan, Laos, *LK-232* (AB610228); Sekong, Laos, *LK-237* (AB610222); Attapeu, Laos, *LK-241* (AB610223); Kaeng Koo rapid, Vapay District, Salavan, Laos, *M. Kato, S. Koi & T. Wongrasert LK-406* (TNS, LC151297); Se Sad river, Ban Bueng Sai, Salavan, Laos, *M. Kato, S. Koi & T. Wongrasert LK-413* (TNS, LC151298); Tad Nam Pa (Tad Jo) waterfall, Ban Xan Sai, Attapeu, Laos, *M. Kato, S. Koi & T. Wongrasert LK-419* (TNS, LC151299); Tad Sa Mong Phak waterfall, Se Pian National Protected Area, Attapeu, Laos, *M. Kato, S. Koi & T. Wongrasert LK-423* (TNS, LC151300); Tad Soy rapid, Se Pian National Protected Area, Attapeu, Laos, *M. Kato, S. Koi & T. Wongrasert LK-429* (TNS, LC151301); Se Lamong stream, Dong Ampham National Protected Area, Attapeu, Laos, *M. Kato, S. Koi & T. Wongrasert LK-433* (TNS, LC151302); Tad Champy waterfall, Champasak, Laos, *M. Kato, S. Koi & T. Wongrasert LK-438* (TNS, LC151303); Champasak, Laos, *LKF-103* (AB537379); Champasak, Laos, *LKF-109* (AB610217); Salavan, Laos, *LKF-118* (AB537380); Champasak, Laos, *LKF-120* (AB610218); Pang Sida National Park, Mantara waterfall, Sa Kao, southeastern Thailand, *P. Werukamkul & L. Ampornpan SK-04* (BKF, TNS, LC151304); Suanman Suantong waterfall, Sa Kao, southeastern Thailand, *P. Werukamkul & L. Ampornpan SK-06* (BKF, TNS); Khwae Makha waterfall, Sa Kao, southeastern Thailand, *P. Werukamkul & L. Ampornpan SK-07* (BKF, TNS); Kaeng Dan Krating, Sa Kao, southeastern Thailand, *P. Werukamkul & L. Ampornpan SK-08* (BKF, TNS, LC151305). *Cladopus queenslandicus* (Domin) C. D. K. Cook & Rutish.—Queensland, Australia, *AU-01* (AB038199); Central, Papua New Guinea, *H. Akiyama 16803* (AB300702). *Cladopus taiensis* C. Cusset—Forest Protection Phu Khiew Unit5, Nong Bua Daeng, Chaiyaphum, Thailand, *P. Werukamkul & L. Ampornpan CP-09* (BKF, TNS, LC151306); Kaeng Wang Konsak, Nong Bua Daeng, Thailand, *P. Werukamkul & L. Ampornpan CP-26* (BKF, TNS, LC151307); Kaeng Paktok, Nong Bua Daeng, Thailand, *P. Werukamkul & L. Ampornpan CP-31* (BKF, TNS, LC151308); Nakhon Nayok, Thailand, *TL-101* (AB048372); Nakhon Nayok, Thailand, *TL-102* (AB698212); Nakhon Nayok, Thailand, *TL-604* (AB698213); Forest Protection Phu Khiew Unit5, Nong Bua Daeng, Chaiyaphum, Thailand, *M. Kato, S. Koi, P. Werukamkul & L. Ampornpan TL-1903* (BKF, TNS, LC151309). *Hanseniella heterophylla* C. Cusset—Phitsanulok, Thailand, *TL-311* (AB104562); Loei, Thailand, *TL-1104* (AB537388); Loei, Thailand, *TPK-13* (AB610229); Loei, Thailand, *TPK-15* (AB610230); Kaeng Huataek, Nakhon Thai, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-211* (BKF, TNS, LC151310); Tadtam waterfall, Phu Kad Wildlife Sanctuary, Nakhon Thai, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-228* (BKF, TNS, LC151311); Tadtinmee waterfall, Nakhon Thai, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-229* (BKF, TNS, LC151312); Wanglum waterfall, Nakhon Thai, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-231* (BKF, TNS, LC151313); Kaeng Moradokpa, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-236* (BKF, TNS, LC151314); Kaeng Hinlad, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-237* (BKF, TNS, LC151315); Kaeng Ratchamoung, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-238* (BKF, TNS, LC151407); Kaeng Sang, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-239* (BKF, TNS, LC151408); Kaeng Sopharam, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-240* (BKF, TNS, LC151316); Kaeng Yao, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-241* (BKF, TNS, LC151317); Kaeng Sai, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-242* (BKF, TNS, LC151318); Poi waterfall, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-243* (BKF, TNS, LC151319); Kaeng Tin Thai Lang, Wang

- Thong, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TWA-246* (BKF, TNS, LC151320); Kaeng S P Hut, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TWA-248* (BKF, TNS, LC151321); Kaeng Kukla, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TWA-249* (BKF, TNS, LC151322); Kaeng Pa-khao Krayang, Wang Thong, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TWA-251* (BKF, TNS, LC151323); Tintok waterfall, Nakhon Thai, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TWA-260* (BKF, TNS, LC151324); Kaeng Hom, Thung Salaeng Luang National Park, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TWA-331* (BKF, TNS, LC151325). ***Hydrobryum austrolaoticum*** Koi & M. Kato—Champasak, Laos, LK-116 (AB610232); Champasak, Laos, LK-122 (AB610233); Champasak, Laos, LK-125 (AB610234); Champasak, Laos, LKF-104 (AB537417); Champasak, Laos, LKF-106 (AB610231); Salavan, Laos, LKF-115 (AB537418). ***Hydrobryum bifoliatum*** C. Cusset—Phitsanulok, Thailand, TL-310 (AB104564). ***Hydrobryum chiangmaiense*** M. Kato—Pu Huen waterfall, Fang, Chiang Mai, Thailand, *P. Werukamkul* & *L. Ampornpan CM-11* (BKF, TNS, LC151326); loc. cit., *P. Werukamkul* & *L. Ampornpan CM-12* (BKF, TNS, LC151327); A stream on the way from Mae Kampong village to Jae Sorn waterfall, Mae On, Chiang Mai, Thailand, S. Koi & T. Wongprasert TK-06 (TNS, LC155826); Lampang, Thailand, TK-07 (AB537389); Chiang Mai, Thailand, TL-63 (AB048373); Chiang Mai, Thailand, TL-64 (AB698245); Chiang Mai, Thailand, TL-65 (AB537390); Chiang Mai, Thailand, TL-421 (AB698246); Chiang Mai, Thailand, TL-422 (AB537391); Chiang Mai, Thailand, TL-423 (AB698247); Chiang Mai, Thailand, TL-424 (AB537392); Chiang Mai, Thailand, TL-425 (AB698248); Chiang Mai, Thailand, TL-428 (AB537393); Chiang Mai, Thailand, TL-429 (AB104570); Chiang Mai, Thailand, TL-430 (AB698241); Chiang Mai, Thailand, TL-431 (AB698242); Chiang Mai, Thailand, TL-432 (AB698243); Chiang Mai, Thailand, TL-801 (AB537394); Chiang Mai, Thailand, TL-807 (AB698249); Chiang Mai, Thailand, TL-1707 (AB698244); Ban Mae Kampong, King Amphoe Mae On, Chiang Mai, Thailand, M. Kato & S. Koi TL-1801 (BKF, TNS, LC151328). ***Hydrobryum chompuense*** Ampornpan, Werukamkul, M. Kato & Koi—Kaeng Tham Namnoi, Tung Salaeng Luang National Park, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TPK-205* (BKF, TNS); loc. cit., *P. Werukamkul* & *L. Ampornpan TWA-337* (BKF, TNS, LC155830); Kaeng Hinlad, Tung Salaeng Luang National Park, Phitsanulok, Thailand, *P. Werukamkul* & *L. Ampornpan TPK-206* (BKF, TNS). ***Hydrobryum floribundum*** Koidz.—Kagoshima, Japan, JK-Anraku2 (AB104571); Kagoshima, Japan, JK-Mae (AB104571). ***Hydrobryum griffithii*** (Wall. ex Griff.) Tul.—Yunnan, China, CH-102 (AB104568); Chiang Mai, Thailand, TL-205 (AB104569). ***Hydrobryum japonicum*** Imamura—Yunnan, China, CH-101 (AB104573); Ban Mae Sa, Mae Chaem, Chiang Mai, Thailand, *P. Werukamkul* & *L. Ampornpan CM-02* (BKF, TNS, LC151329); Ban Sop Mae Sa, Mae Chaem, Chiang Mai, Thailand, *P. Werukamkul* & *L. Ampornpan CM-03* (BKF, TNS, LC151330); Ban Sop Mae Ruam, Mae Chaem, Chiang Mai, Thailand, *P. Werukamkul* & *L. Ampornpan CM-04* (BKF, TNS, LC151331); Ban Muang Chum, Fang, Chiang Mai, Thailand, *P. Werukamkul* & *L. Ampornpan CM-16* (BKF, TNS, LC151332); Ban Mae Fangluang, Chai Prakan, Chiang Mai, Thailand, *P. Werukamkul* & *L. Ampornpan CM-17* (BKF, TNS, LC151333); loc. cit., *P. Werukamkul* & *L. Ampornpan CM-18* (BKF, TNS, LC151334); loc. cit., *P. Werukamkul* & *L. Ampornpan CM-19* (BKF, TNS, LC151335); Osumi Peninsula, Kagoshima, Japan, JK-01 (AB038192); Kachin, Myanmar, J. Murata & al. 041232 (AB537396); Oudom Xai, Laos, LK-301 (AB698250); Luang Namtha, Laos, LK-302 (AB698251); Luang Namtha, Laos, LK-303 (AB698252); Luang Namtha, Laos, LK-304 (AB698253); Luang Namtha, Laos, LK-305 (AB698254); Luang Namtha, Laos, LK-306 (AB698255); Luang Namtha, Laos, LK-308 (AB698256); Bokeo, Laos, LK-318 (AB698257); Phetchaburi, Thailand, TIF-115 (AB698258); Chiang Mai, Thailand, TK-01 (AB610235); Chiang Mai, Thailand, TK-03 (AB698259); Chiang Mai, Thailand, TK-08 (AB698262); Loei, Thailand, TKF-09 (AB698264); Chiang Mai, Thailand, TL-206 (AB698265); Chiang Mai, Thailand, TL-415 (AB537397); Chiang Mai, Thailand, TL-420 (AB537398); Chiang Mai, Thailand, TL-426 (AB698266); Chiang Mai, Thailand, TL-427 (AB537399); Chiang Mai, Thailand, TL-1004 (AB698267); Mae Hongson, Thailand, TL-1006 (AB698268); Loei, Thailand, TL-1103 (AB537400); Chiang Mai, Thailand, TL-1201 (AB698269); Mae Hongson, Thailand, TL-1203 (AB698270); Mae Hongson, Thailand, TL-1204 (AB698271); Chiang Mai, Thailand, TL-1701 (AB698272); Chiang Mai, Thailand, TL-1702 (AB698260); Chiang Mai, Thailand, TL-1705 (AB698261); Chiang Mai, Thailand, TL-1708 (AB698263); Tadnoi waterfall, Forest Protection Ban Namjan Unit, Wang Saphung, Loei, Thailand, M. Kato, S. Koi, *P. Werukamkul* & *L. Ampornpan TL-1906* (BKF, TNS, LC151336); loc. cit., M. Kato, S. Koi, *P. Werukamkul* & *L. Ampornpan TL-1907* (BKF, TNS, LC151337); loc. cit., M. Kato, S. Koi, *P. Werukamkul* & *L. Ampornpan TL-1908* (BKF, TNS, LC151338); loc. cit., *P. Werukamkul* & *L. Ampornpan TWA-284* (BKF, TNS, LC151340); Namjan waterfall, Forest Protection Ban Namjan Unit, Wang Saphung, Loei, Thailand, M. Kato, S. Koi, *P. Werukamkul* & *L. Ampornpan TL-1909* (BKF, TNS, LC151339); loc. cit., *P. Werukamkul* & *L. Ampornpan TWA-289* (BKF, TNS, LC151341); Pha Lad waterfall, Mae Ruam, Mae Takhrui National Park, Mae On, Chiang Mai, Thailand, S. Koi, *P. Werukamkul* & *L. Ampornpan TPK-101* (BKF, TNS, LC151342); Sapa, Vietnam, Viel (AB610236). ***Hydrobryum kaengsophense*** M. Kato—Phitsanulok, Thailand, TL-312 (AB104565). ***Hydrobryum khaoyaiense*** M.

- Kato—Mantara waterfall, Pang Sida National Park, Sa Kao, Thailand, *P. Werukamkul & L. Ampornpan SK-05* (BKF, TNS, LC151343); Kaeng Dan Krating, Pang Sida National Park, Sa Kao, Thailand, *P. Werukamkul & L. Ampornpan SK-09* (BKF, TNS, LC151344); Kaeng klong Munao, Pang Sida National Park, Sa Kao, Thailand, *P. Werukamkul & L. Ampornpan SK-10* (BKF, TNS, LC151345); Nakhon Nayok, Thailand, *TIF-53* (AB698273); Nakhon Nayok, Thailand, *TK-09* (AB537395); Nakhon Nayok, Thailand, *TKF-26* (AB698274). *Hydrobryum koribanum* Imamura ex Nakayama & Minamitani—Miyazaki, Japan, *JK-05* (AB048374). *Hydrobryum loeicum* M. Kato—Loei, Thailand, *TKF-06* (AB698275); Loei, Thailand, *TKF-07* (AB698276); Loei, Thailand, *TKF-08* (AB698277); Loei, Thailand, *TL-209* (AB698278); Loei, Thailand, *TL-210* (AB104566); Loei, Thailand, *TL-211* (AB537401); Loei, Thailand, *TPK-06* (AB698279); Loei, Thailand, *TPK-10* (AB698280); Had San, Na Hao, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-261* (BKF, TNS, LC151346); Kaeng Kontone, Na Hao, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-262* (BKF, TNS, LC151347); Tatkoey waterfall, Na Hao, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-263* (BKF, TNS, LC151348); Kaeng Thakam, Na Hao, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-311* (BKF, TNS, LC151349); Tat Hueang waterfall, Na Hao, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-356* (BKF, TNS, LC151350). *Hydrobryum luangnamtaense* Koi & M. Kato—Luang Namtha, Laos, *LK-313* (AB698284); Luang Namtha, Laos, *LK-314* (AB698285); Luang Namtha, Laos, *LK-315* (AB698286); Luang Namtha, Laos, *LK-316* (AB698287); Luang Namtha, Laos, *LK-317* (AB698288). *Hydrobryum mandaengense* Ampornpan, Werukamkul, M. Kato & Koi—Mandaeng waterfall, Phu Hin Rong Kla National Park, Nakhon Thai, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-198* (BKF, TNS, LC155827); *loc. cit.*, M. Kato, S. Koi, P. Werukamkul, & L. Ampornpan *TL-1913* (BKF, TNS, LC158663). *Hydrobryum micrantherum* var. *crassum* M. Kato—Nakhon Nayok, Thailand, *TL-57* (AB038205); Nakhon Nayok, Thailand, *TL-58* (AB104574); Nakhon Nayok, Thailand, *TL-306* (AB104576). *Hydrobryum micrantherum* var. *micrantherum* (P. Royen) C. D. K. Cook & Rutish.—Chanthaburi, Thailand, *TL-62* (AB104575); Chanthaburi, Thailand, *TL-1505* (AB698281). *Hydrobryum phetchabunense* M. Kato & Koi—Santisuk waterfall, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-32* (BKF, TNS, LC151351); Phetchabun, Thailand, *TKF-01* (AB537414); Phetchabun, Thailand, *TL-1102* (AB537415); Kaeng Lad waterfall, Nakhon Thai, Phitsanulok, Thailand, M. Kato, S. Koi, P. Werukamkul & L. Ampornpan *TL-1911* (BKF, TNS, LC151352); *loc. cit.*, P. Werukamkul & L. Ampornpan *TWA-176* (BKF, TNS, LC151353); Kaeng Hak Piree, Thung Salaeng Luang National Park, Phetchabun, Thailand, M. Kato, S. Koi, P. Werukamkul & L. Ampornpan *TL-1914* (BKF, TNS, LC151354); Sridit waterfall, Khao Kho Non-hunting area, Phetchabun, Thailand, M. Kato, P. Werukamkul & L. Ampornpan *TL-2006B* (BKF, TNS, LC151355); *loc. cit.*, M. Kato, P. Werukamkul & L. Ampornpan *TL-2006C* (BKF, TNS, LC151356); Pha Lad waterfall, Phu Hin Rong Kla National Park, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-200* (BKF, TNS, LC151357); Kaeng Sapung waterfall, Nakhon Thai, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-202* (BKF, TNS, LC151358); Kaeng Hin Sai waterfall, Nakhon Thai, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-203* (BKF, TNS, LC151359); Tadyai waterfall, Nakhon Thai, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-230* (BKF, TNS, LC151360); Huai Taleo waterfall, Nakhon Thai, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-232* (BKF, TNS, LC151361); Pha Tairuea waterfall, Nakhon Thai, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-252* (BKF, TNS, LC151362); Wanglum waterfall, Nakhon Thai, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-253* (BKF, TNS, LC151363); *loc. cit.*, P. Werukamkul & L. Ampornpan *TWA-254* (BKF, TNS, LC151364); Kaeng Kana, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-267* (BKF, TNS, LC151365); Kaeng Wang Tham Sang, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-277* (BKF, TNS, LC151366); Kaeng Pak Khlong Khunkajak, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-280* (BKF, TNS, LC151367); Kaeng Wang Takian, Tung Salaeng Luang National Park, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-332* (BKF, TNS, LC151368); Kaeng Tham Namnoi, Tung Salaeng Luang National Park, Phitsanulok, Thailand, P. Werukamkul & L. Ampornpan *TWA-336* (BKF, TNS, LC151369). *Hydrobryum phurueanum* Werukamkul, Ampornpan, Koi & M. Kato—Loei, Thailand, *TPK-16* (AB610251). *Hydrobryum puncticulatum* Koidz.—Kagoshima, Japan, *JK-Yaku* (AB104572). *Hydrobryum ramosum* (C. Cusset) Koi & M. Kato—Vientiane, Laos, *LK-05* (AB537383); Vientiane, Laos, *LKF-05* (AB610237). *Hydrobryum somranii* M. Kato—Huai Khaml, Phu Langka National Park, Nakhon Phanom, Thailand, P. Werukamkul & L. Ampornpan *NE-37* (BKF, TNS, LC151370); Huai Kloi, Phu Langka National Park, Nakhon Phanom, Thailand, P. Werukamkul & L. Ampornpan *NE-40* (BKF, TNS, LC151371); Nakhon Phanom, Thailand, *TL-703* (AB537402); Nakhon Phanom, Thailand, *TL-704* (AB537403). *Hydrobryum subcrustaceum* Koi & M. Kato—Vientiane, Laos, *L-15* (AB537408); Vientiane, Laos, *LK-03* (AB537409); Vientiane, Laos, *LKF-02* (AB537410); Vientiane, Laos, *LKF-04*

(AB537411). *Hydrobryum subcylindricum* Koi & M. Kato—Bolikhamsai, Laos, *L-09* (AB537405); Bolikhamsai, Laos, *L-13* (AB610238); Bolikhamsai, Laos, *LKF-17* (AB537406). *Hydrobryum taeniatum* Koi & M. Kato—Bolikhamsai, Laos, *L-08* (AB537404); Bolikhamsai, Laos, *LK-107* (AB610239). *Hydrobryum takakioides* Koi & M. Kato—Bolikhamsai, Laos, *L-14* (AB610240); Bolikhamsai, Laos, *LK-202* (AB610241); Bolikhamsai, Laos, *LKF-16* (AB537407). *Hydrobryum tardhuangense* M. Kato—Khammouan, Laos, *LK-113* (AB610242); Kaeng Songkran, Khao Kho, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-16* (BKF, TNS, LC151372); Kaeng Sam, Khao Kho, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-18* (BKF, TNS, LC151373); Kaeng Saehuo, Khao Kho, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-26* (BKF, TNS, LC151374); Kaeng Wang Nam Yen, Thung Salaeng Luang National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-27* (BKF, TNS, LC151375); *loc. cit.*, M. Kato, S. Koi, *P. Werukamkul & L. Ampornpan TL-1916* (BKF, TNS, LC151376); Kaeng Hak Piree, Tung Salaeng Luang National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-28* (BKF, TNS, LC151377); Kaeng Ratchapruet, Khao Kho, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-29* (BKF, TNS, LC151378); *loc. cit.*, *P. Werukamkul & L. Ampornpan PB-44* (BKF, TNS, LC151379); Lanhin Phettara, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-37A* (BKF, TNS, LC151380); Phettara waterfall, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-38* (BKF, TNS, LC151381); Huai Chaliang Haeng1, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-39* (BKF, TNS, LC151382); Kaeng Sam Ngam, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-40A* (BKF, TNS, LC151383); Huai Namdum, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-41* (BKF, TNS, LC151384); Huai Chaliang Haeng2, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-42* (BKF, TNS, LC151385); Phetnaiprai waterfall, Khao Kho National Park, Phetchabun, Thailand, *P. Werukamkul & L. Ampornpan PB-43* (BKF, TNS, LC151386); Loei, Thailand, *TL-208* (AB104567); Water Turbine, Phu Hin Rong Kla National Park, Phitsanulok, Thailand, M. Kato, S. Koi, *P. Werukamkul & L. Ampornpan TL-1912* (BKF, TNS, LC151387); *loc. cit.*, *P. Werukamkul & L. Ampornpan TWA-199* (BKF, TNS, LC155828); Sridit Waterfall, Khao Kho Non-hunting area, Phetchabun, Thailand, M. Kato, *P. Werukamkul & L. Ampornpan TL-2006A* (BKF, TNS, LC151388); Kaeng Bang Rachan, Tung Saleng Luang National Park, Phetchabun, Thailand, M. Kato, *P. Werukamkul & L. Ampornpan TL-2007* (BKF, TNS, LC151389); *loc. cit.*, M. Kato, *P. Werukamkul & L. Ampornpan TL-2009* (BKF, TNS, LC151390); Romklao Pharadon Waterfall, Phu Hin

Rong Kla National Park, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-201* (BKF, TNS, LC155829); Kaeng Thakam, Na Haeo, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-310* (BKF, TNS, LC151391); Kaeng Sopha waterfall, Tung Saleng Luang National Park, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-328* (BKF, TNS, LC151392). *Hydrobryum varium* Ampornpan, Werukamkul, Koi & M. Kato—Loei, Thailand, *TPK-22* (AB610252); Huai Phai waterfall, Huai Phai National Park, Loei, Thailand, *P. Werukamkul & L. Ampornpan TWA-113* (BKF, TNS); *loc. cit.*, *P. Werukamkul & L. Ampornpan TWA-114* (BKF, TNS). *Hydrobryum verrucosum* Koi & M. Kato—Bolikhamsai, Laos, *L-07* (AB537412); Bolikhamsai, Laos, *L-12* (AB610243); Bolikhamsai, Laos, *LK-105* (AB610244); Bolikhamsai, Laos, *LKF-14* (AB537413). *Hydrobryum vientianense* (M. Kato & Fukuoka) Koi & M. Kato—Vientiane, Laos, *L-01* (AB537384); Vientiane, Laos, *L-02* (AB610245); Vientiane, Laos, *L-16* (AB537385); Vientiane, Laos, *LK-06* (AB537386); Vientiane, Laos, *LK-07* (AB610246); Vientiane, Laos, *LK-08* (AB537387); Loei, Thailand, *TKF-02* (AB537416); Loei, Thailand, *TKF-04* (AB698282); Loei, Thailand, *TPK-24* (AB698283); Loei, Thailand, *TPK-26A* (AB610247); Loei, Thailand, *TPK-26B* (AB610248); Loei, Thailand, *TPK-28* (AB610249); Loei, Thailand, *TPK-29* (AB610250). *Hydrobryum cf. vientianense*—Loei, Thailand, *TPK-01* (AB610253). *Hydrodiscus koyamae* (M. Kato & Fukuoka) Koi & M. Kato—Bolikhamsai, Laos, *L-06* (AB537381); Bolikhamsai, Laos, *L-11* (AB537382); Bolikhamsai, Laos, *LK-104* (AB610255); Bolikhamsai, Laos, *LKF-13* (AB610254). *Paracladopus chanthaburiensis* Koi & M. Kato—Chanthaburi, Thailand, *TIK-21* (AB293559); Chanthaburi, Thailand, *TIK-34* (AB300701); Chanthaburi, Thailand, *TKF-24* (AB698346); Chanthaburi, Thailand, *TL-1533* (AB293558). *Paracladopus chiangmaiensis* M. Kato—Mae Wang river, Mae Wang, Chiang Mai, Thailand, *P. Werukamkul & L. Ampornpan CM-07* (BKF, TNS, LC151393); Pha Lad waterfall, Mae Wang, Chiang Mai, Thailand, *P. Werukamkul & L. Ampornpan CM-08* (BKF, TNS, LC151394); Champasak, Laos, *LK-213* (AB610258); Champasak, Laos, *LK-220* (AB610259); Champasak, Laos, *LK-223* (AB611703); Champasak, Laos, *LKF-105* (AB610256); *LKF-110* (AB537419); *LKF-116* (AB610257); *LKF-119* (AB537420); Champasak, Laos, *LKF-121* (AB537421); Vietnam, S.-W. *Chung s.n.* (Vie2) (AB698348); Chiang Mai, Thailand, *TK-201* (AB698347); Chiang Mai, Thailand, *TL-808* (AB293560); Chiang Mai, Thailand, *TL-1706* (AB537422); Wang Thantong waterfall, Chiang Khong, Chiang Rai, Thailand, S. Koi, *P. Werukamkul & L. Ampornpan TPK-106* (BKF, TNS, LC151395). *Thawatchaia laotica* Koi & M. Kato—Kaeng Yung, Kok river, Mae Ai, Chiang Mai, Thailand, *P. Werukamkul & L. Ampornpan CM-13* (BKF, TNS, LC151396); *loc. cit.*, S. Koi, *P. Werukamkul & L. Ampornpan TPK-103* (BKF, TNS, LC151397); Luang

Namtha, Laos, *LK-307* (AB698408); Luang Namtha, Laos, *LK-309* (AB698409); Luang Namtha, Laos, *LK-310* (AB698410); Luang Namtha, Laos, *LK-312* (AB698411); Bokeo, Laos, *LK-319* (AB698412). *Thawatchaia trilobata* M. Kato, Koi & Y. Kita—Mae Wang waterfall, Mae Wang, Chiang Mai, Thailand, *P. Werukamkul & L. Ampornpan CM-05* (BKF, TNS, LC151398); Mae Wang river, Mae Wang, Chiang Mai, Thailand, *P. Werukamkul & L. Ampornpan CM-06* (BKF, TNS, LC151399); Pha Lad waterfall, Mae Wang, Chiang Mai, Thailand, *P. Werukamkul & L. Ampornpan CM-10* (BKF, TNS, LC151400); Chiang Mai, Thailand, *TL-419* (AB104563); Chiang Mai, Thailand, *TL-804* (AB698413); Chiang Mai, Thailand, *TL-809* (AB698414); Loei, Thailand, *TPK-02* (AB610474); Loei, Thailand, *TPK-04* (AB610475); Loei, Thailand, *TPK-07* (AB698415); Loei, Thailand, *TPK-14* (AB610476); Kaeng Kana, Khlong Chompu Stream, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, *P.*

Werukamkul & L. Ampornpan TWA-268 (BKF, TNS, LC151401); Kaeng Pak Kasao, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-271* (BKF, TNS, LC151402); Kaeng Wang Kadum, Tung Salaeng Luang National Park Noen Maprang, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-275* (BKF, TNS, LC151403); Kaeng Wang Tham Sang, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-278* (BKF, TNS, LC151404); Kaeng Pak Klong Khunkrajiak, Tung Salaeng Luang National Park, Noen Maprang, Phitsanulok, Thailand, *P. Werukamkul & L. Ampornpan TWA-281* (BKF, TNS, LC151405); Kaeng Wang Takian, Tung Salaeng Luang National Park, Noen Maprang, Thailand, *P. Werukamkul & L. Ampornpan TWA-333* (BKF, TNS, LC151406).
